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Species–area relationships are modulated by trophic rank, habitat affinity, and dispersal ability

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Abstract. In the face of ongoing habitat fragmentation, species–area relationships (SARs) have gained renewed interest and are increasingly used to set conservation priorities. An important question is how large habitat areas need to be to optimize biodiversity conservation. The relationship between area and species richness is explained by colonization–extinction dynamics, whereby smaller sites harbor smaller populations, which are more prone to extinction than the larger populations sustained by larger sites. These colonization–extinction dynamics are predicted to vary with trophic rank, habitat affinity, and dispersal ability of the species. However, empirical evidence for the effect of these species characteristics on SARs remains inconclusive.

In this study we used carabid beetle data from 58 calcareous grassland sites to investigate how calcareous grassland area affects species richness and activity density for species differing in trophic rank, habitat affinity, and dispersal ability. In addition, we investigated how SARs are affected by the availability of additional calcareous grassland in the surrounding landscape.

Beetle species richness and activity density increased with calcareous grassland area for zoophagous species that are specialists for dry grasslands and, to a lesser extent, for zoophagous habitat generalists. Phytophagous species and zoophagous forest and wet-grassland specialists were not affected by calcareous grassland area. The dependence of species on large single sites increased with decreasing dispersal ability for species already vulnerable to calcareous grassland area. Additional calcareous grassland in the landscape had a positive effect on local species richness of both dry-grassland specialists and generalists, but this effect was restricted to a few hundred meters.

Our results demonstrate that SARs are affected by trophic rank, habitat affinity, and dispersal ability. These species characteristics do not operate independently, but should be viewed in concert. In addition, species' responses depend on the landscape context. Our study suggests that the impact of habitat area on trophic interactions may be larger than previously anticipated. In small habitat fragments surrounded by a hostile matrix, food chains may be strongly disrupted. This highlights the need to conserve continuous calcareous grassland patches of at least several hectares in size.

Key words: biodiversity conservation; body size; calcareous grasslands; carabid beetles; community; flight ability; food chain; fragmentation; generalist vs. specialist; northwestern Europe; SAR; trophic level.

INTRODUCTION

Species–area relationship (SAR) theory predicts that species richness increases with area (Williams 1943, Preston 1960, MacArthur and Wilson 1967). There are two main ecological mechanisms underlying this long-standing and rigorously tested ecological theory, which are not mutually exclusive. First, large areas tend to contain a larger diversity of environmental conditions and biotopes, which support a greater variety of species (Williams 1964), because species differ in resource

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requirements and environmental tolerance to abiotic conditions. This is called the “habitat–diversity hypothesis.” The second mechanism, termed the “area per se hypothesis,” is derived from the extinction–colonization equilibrium underlying classical island biogeography theory (MacArthur and Wilson 1967). Extinction rates increase with decreasing population size (Hanski 1999, Henle et al. 2004) and population density generally increases or remains constant with increasing area (Connor et al. 2000). This implies that small sites harbor small populations, which are more prone to extinction than the large populations sustained by large sites. SARs have recently received renewed interest in the light of conservation ecology and are increasingly used to predict extinction rates of target species for nature conservation (e.g., Hanski et al. 2013) and to prioritize conservation efforts (e.g., Steffan-Dewenter and Tscharntke 2000). An important question in this respect is how large habitat areas need to be to optimize biodiversity conservation.

The minimum area of habitat required to support a viable community relates to the area per se hypothesis, which predicts that SARs depend on species-specific colonization–extinction dynamics. Extinction rates decrease with habitat area (MacArthur and Wilson 1967), whereas colonization rates are predicted to decrease with habitat isolation (MacArthur and Wilson 1967). This implies that SARs are also affected by the landscape context (Hanski 1999, Hanski et al. 2013). Additional habitat in the landscape will increase metapopulation persistence and, hence, colonization chances (Hanski 1999). Here it is worth noting that SAR theory was initially developed for real islands, where the surrounding matrix (i.e., non-habitat landscape) is clearly inhospitable for all terrestrial species. When applying these principles to “islands” of a specific biotope (e.g., calcareous grassland) surrounded by other land use types (e.g., arable land), the role of the matrix becomes more complex (Haila 2002, Shepherd and Brantley 2005). Although the matrix may be hostile and unsuitable for specialist species, which perceive their habitat as fragmented, the landscape may provide continuous habitat for generalist species (Driscoll et al. 2013). A species’ habitat affinity is thus likely to alter its response to biotope area and site isolation (De Vries et al. 1996, Davies et al. 2000, Swihart et al. 2003).

In addition to habitat affinity, which influences how species perceive the landscape, there are a number of other factors that affect extinction–colonization dynamics. Colonization rates increase with increasing dispersal ability (Den Boer 1990a, Tscharntke et al. 2002a). Extinction rates are determined by several species characteristics (Verberk et al. 2010), including body size (Damuth 1981, Stork and Blackburn 1993) and trophic rank (Holt et al. 1999). Body size has repeatedly been identified as a trait that negatively affects population density, but the cause of this pattern is debatable because size is correlated with

several other traits affecting population density, including trophic rank (Tscharntke et al. 2002a, Henle et al. 2004). Trophic rank affects extinction rates because species from higher trophic ranks (carnivores and parasites) generally have both lower population densities (Henle et al. 2004, Verberk et al. 2010) and increased population fluctuations (Holt et al. 1999, Tscharntke and Kruess 1999, Henle et al. 2004, Van Nouhuys 2005). The rationale behind this is that less energy is transferred through successive links in the food chain, causing predators to be less abundant than prey of comparable body size and reproductive rate (Hutchinson 1959, Heino 2008). In addition, populations of higher trophic rank are likely to exhibit stronger numerical fluctuations, because fluctuations of food (or prey or host) sources are exacerbated as they cascade up the food chain (Holt et al. 1999, Van Nouhuys 2005). Despite this theoretical underpinning, empirical evidence for the effect of trophic rank on the SAR has been inconsistent (Van Nouhuys 2005) and it has been suggested that increasing SAR slopes with increasing trophic rank should be limited to food specialists (Steffan-Dewenter and Tscharntke 2002, Henle et al. 2004). A complicating factor is that most studies to date have been carried out in plant–herbivore and host–parasite systems (Tscharntke et al. 2002b, Van Nouhuys 2005), where the species belonging to different trophic ranks also differ in other respects. In these cases, differences in body size and dispersal ability between trophic ranks may alternatively explain observed patterns, rather than trophic rank per se.

In this study we aim first to investigate how the area of a biotope affects species richness of a single monophyletic taxon that includes species differing in trophic rank, dispersal ability, and habitat affinity. Second, we investigate how SARs for this taxon are affected by habitat isolation. We use carabid beetles as a focal group because their ecology has been widely studied (Koivula 2011, Kotze et al. 2011) and they exhibit considerable variation in trophic rank, dispersal ability, and habitat affinity (Turin 2000). This provides a unique opportunity to study the effect of trophic rank on SAR, independent of major body plan constraints. We performed this study in calcareous grasslands because this habitat is of high conservation value (WallisDeVries et al. 2002) and has become highly fragmented over the past century across Europe (Baldock et al. 1996, WallisDeVries et al. 2002). Using a meta-analysis of data sets from northwestern Europe, we test the hypothesis that carabid beetle species richness will increase with calcareous grassland area. Because we expect that such increases are caused by an increase in population viability (following the area per se hypothesis), we expect carabid beetle activity density to also increase. We hypothesize that the minimum area required for viable populations increases with trophic level due to decreased population density and stability.

TABLE 1. Specifications of the carabid beetle data sets included in the analysis.

Set no.	Country	No. sites	No. traps/site	Trap diameter (cm)	Season	Trapping duration (d)	Year	Method reference	Symbol in Figs. 1 and 2
1	Germany	3	20	8.5	Apr–Oct	200	2006	van Noordwijk et al. (2012)	circle
2	Netherlands	15	10	8.5	Apr–Oct	200	1988	van Noordwijk et al. (2012)	triangle
3	Germany	4	10	8.5	Mar–Oct	220	1986 or 1987	Eckel (1988)	plus
4	Germany	4	15–20	9	all year	730	1995 and 1996	Hannig et al. (2005)	open square
5	Ireland	19	10	7 and 9	May–Aug	55	2006	E. Regan, <i>personal communication</i>	solid square
6	Belgium	13	10	8.5	Apr–Oct	185	1986 or 1987	Dufrène (1990)	star

This should cause zoophagous species to respond more strongly than phytophagous species to biotope area. We also predict that flightless species (see Plate 1) will be restricted to larger sites than species possessing good flight ability and that additional calcareous grassland in the surrounding landscape will positively affect carabid beetle richness in accordance with metapopulation theory (Hanski 1999). Given the differences between species in their perception of the landscape, we hypothesize that all of these patterns will be contingent upon the habitat affinity of a species. These predictions should only hold for dry-grassland specialists, whereas habitat generalists and typical species of wet grasslands and forests will not be affected by the area of calcareous grassland.

METHODS

Study system

Calcareous grasslands in northwestern Europe have a distinct carabid beetle fauna, consisting mainly of thermophilic species, which are restricted to nutrient-poor grasslands with a relatively warm microclimate (Lindroth 1949). In addition, calcareous grasslands are inhabited by eurytopic species, which may also occur in various arable and grassland habitats (Turin 2000). Large parts of northwestern Europe have seen a sharp decline in the area and quality of calcareous grassland over the past century (Baldock et al. 1996, Wallis-DeVries et al. 2002). Remaining sites are mostly surrounded by arable land, fertilized grasslands, and woodland.

Carabid beetle data collection

We collected six data sets from four countries containing pitfall trap data of carabid beetles from unimproved (unfertilized) calcareous grasslands (58 sites; see Appendix A for details). Descriptions of the sampling regions and vegetation types of these data sets are given in Eckel (1988), Dufrène (1990), Willems (2001), Hannig et al. (2005); E. Regan and M. J. F. Brown, *unpublished manuscript*. The exact trapping method differed between data sets, but was consistent within each data set (Table 1). For the analyses, all data were pooled for each calcareous grassland site.

Species characteristics

For each species in our data set, we determined trophic rank, habitat affinity, dispersal ability, and mean body size from literature (see Appendix B). We only included those traits and trait categories for which we had reliable data for each species in our data set. Habitat affinity was categorized following Turin (2000) and Desender et al. (2008) with “dry-grassland specialists” defined as all species mainly occurring in dry, nutrient-poor habitats including calcareous grasslands and heathlands, “wet-grassland/forest specialists” defined as species mainly occurring in wet habitats and forests, and “open-habitat generalists” defined as all species occurring in a wide range of open habitats, including agricultural land. We distinguished three trophic groups based on Turin (2000) and Saska (2004, 2005): (1) species that are strictly phytophagous throughout their life cycle (referred to as phytophagous), (2) species that are at least partly zoophagous throughout their life cycle (referred to as zoophagous), and (3) species that are phytophagous as adults, but zoophagous as larvae (referred to as trophic-rank shift). Omnivorous species were grouped together with strictly zoophagous species because we had insufficient information for several species to classify them as either strictly zoophagous or omnivorous (see also Vanbergen et al. 2010). Moreover, most of the species generally classified as being zoophagous also incidentally feed on fruits and other plant material (Thiele 1977). Species that shift from carnivory to herbivory during their life cycle were defined as a separate group. To date, these species have generally been classified as phytophagous species, because most studies only incorporate adult feeding habits (see e.g., Ribera et al. 1999, Vanbergen et al. 2010). We separated these species from the continuously phytophagous species because we suspect that the larva is the most critical stage in the life cycle (Thiele 1977), which would cause these species to behave more like zoophagous species in our analysis. Dispersal ability was classified based on a combination of wing morphology, flight muscle development, and flight records from window traps, following Den Boer (1990b), Turin (2000), and Desender et al. (2008). We distinguished three categories: poor dispersers (species incapable of active flight), intermediate dispersers (species capable of

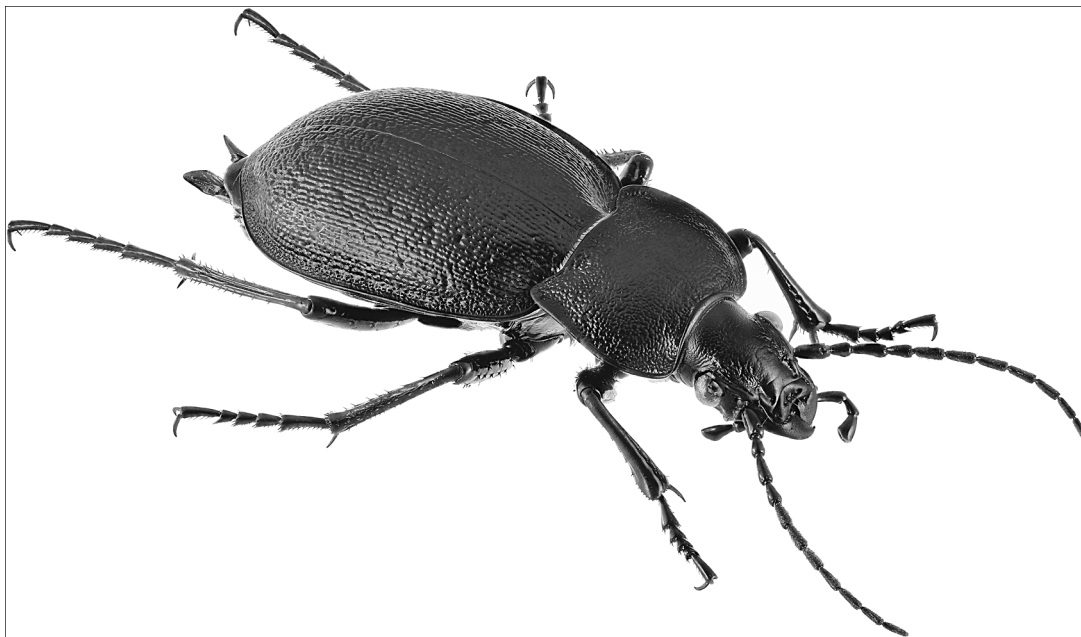


PLATE 1. *Carabus convexus* is a flightless carnivorous carabid beetle which, in northwestern Europe, is restricted to dry grassland habitats. Due to these characteristics it requires large habitat fragments to sustain viable populations. Photo credit: T. Heijerman.

flight, but with few flight records or low proportions of macropterous individuals), and good dispersers (species with a large proportion of the population capable of active flight and regularly caught in window traps). The final species characteristic included in our analysis was body size, measured as the total body length (in mm), which was derived from Turin (2000) and Desender et al. (2008). For statistical analyses, body size was divided into three classes: small (1–6 mm), medium (7–10 mm), and large (11–35 mm), representing similar numbers of species.

GIS analysis

We mapped each calcareous grassland site on aerial images in ArcGIS 9.2 (ESRI, Redlands, California, USA). Where available, we used high-quality free web mapping services (e.g., Bing maps and Google maps). For some of the Irish sites, the quality of freely available aerial photographs was insufficient; instead, we used 1-m resolution orthophotography maps supplied by Ordnance Survey Ireland. On all maps, good-quality (i.e., nutrient-poor, well-managed) calcareous grassland could quite easily be distinguished from other habitat types, including more nutrient-rich or abandoned grassland, due to clear color differences. Site boundaries were always checked by people with field knowledge of the sites. In addition to the sampled sites, we mapped all good-quality calcareous grassland sites in a 1000 m radius around the center point of each sampling site. For each site, we calculated the area of calcareous grassland (m²) within each sampling site and the area of calcareous

grassland within a 500 m and 1000 m radius of the sampling site (excluding the sampling site itself). These spatial scales were chosen because flightless individuals generally do not cover distances of more than a few hundred meters in their lifetime (Den Boer 1970, Thiele 1977).

Statistical analysis

Generalized linear mixed models (GLMM) were used to analyze the data, with data set as a random variable to account for regional differences in carabid beetle assemblage and differences in sampling intensity between data sets. All analyses were performed separately for the three habitat affinity groups: dry-grassland specialists, open-habitat generalists, and wet-grassland and forest specialists. The Irish data set contained only three species classified as dry-grassland specialists, one for each trophic rank (seven individuals in total). Even when adapting habitat affinity criteria to Irish standards, only few species could be characterized as being typical for dry grasslands (Anderson et al. 2000). This is most likely due to the wetter and cooler climate in Ireland, in combination with its impoverished island fauna (Good 2004). For this reason, the Irish data set was excluded from the analysis for typical dry-grassland specialists. For the analyses of generalists and wet-grassland and forest specialists, the Irish data set did not differ structurally from the mainland data sets and hence was included, after checking that the difference in the number of included data sets between habitat affinity groups did not affect the results. We could not construct

TABLE 2. AIC scores for the generalized linear mixed models of carabid beetle species richness per habitat preference group.

Model	Dry-grassland specialists	Open-habitat generalists	Forest and wet-grassland specialists
(Intercept)	244.9	448.2	685.4
Area	238.2	449.4	687.1
Area + 500 m	230.9	437.6	686.1
Area + 1000 m	234.7	446.8	685.8
Area × trophic rank	130.8	182.4	149.6
Area × trophic rank + 500 m	123.1	170.5	148.5
Area × trophic rank + 1000 m	127.5	179.9	148.3

Notes: Data set was included as a random variable in all models. Models within 15 AIC points of the best model are given in bold face. The factors “+ 500 m” and “+ 1000 m” refer to the inclusion of additional calcareous grassland habitat within a 500 m or 1000 m radius, respectively.

a single model including all three species traits (trophic rank, dispersal ability, and body size) because some combinations of trait classes were empty (e.g., there were no large phytophagous species or poorly dispersing phytophagous species). Moreover, all three traits are partly interrelated (Turin 2000, Desender et al. 2008). Instead, we constructed three separate models, demonstrating the effect of each of these traits separately on the SAR. We did this for dry-grassland specialist beetles only, because this was the only habitat affinity group for which we expected an effect of these traits. We then focused primarily on the trait that produced the lowest *P* values (trophic rank) for further analyses on all three habitat affinity groups, but performed additional analyses to ensure that the effects found were not caused by interrelated traits. For trophic rank, models were constructed for two response variables: species richness and activity density (counts of individuals, which are affected by both a species' density and its activity pattern). Activity density data were natural log-transformed to reduce the effect of highly active species (Ribera et al. 2001, Vanbergen et al. 2010). Both species richness and transformed activity density followed a Poisson distribution. All habitat size parameters were natural log-transformed, in accordance with general species–area relationship theory (Connor and McCoy 1979). For both response variables, seven models were constructed (intercept only, calcareous grassland size, and calcareous grassland size × trophic rank, the latter two with no additional landscape parameter, with additional calcareous grassland at the 500-m scale or with additional calcareous grassland at the 1000-m scale), using the lmer function in R package lme4 (Bates et al. 2013). Models were fitted using the Laplace approximation and optimizing the log-likelihood rather than the restricted maximum likelihood (RML) criterion, as this method is better suited when comparing models with varying fixed effects. Because the random part of the seven models was identical, AIC scores could be used to rank models. Model-averaging over all models scoring within 15 AIC points of the best model was used to obtain parameter estimates and significance values (Bolker et al. 2009). To ensure that reported effects of trophic rank were indeed caused by this trait

and not by colinearity between trophic rank and dispersal ability, we also established whether trophic rank had an effect on SAR within the group of dry-grassland carabid beetles with medium and good dispersal ability. The number of medium and good dispersers was equal across trophic ranks, eliminating the colinearity encountered when including poor dispersers, which were all zoophagous. To do this, we used a GLMM analysis (calcareous grassland size × trophic rank) with identical specifications as described previously. Finally, we tested for an independent effect of flight ability, by analyzing the effect of this trait within trophic rank categories. Because the number of species for each dispersal group was rather low within some habitat affinity and trophic rank categories, we could not use a similar GLMM test here. Instead, we tested whether the range of calcareous grassland sizes in which species were found differed between dispersal ability groups, providing an indication of the area requirements of each group. To do this, we used Levene's test (centered round the median rather than the mean of each group, to account for slight deviations from a normal distribution), because we were interested in the range of site sizes, rather than the mean size of sites in which species of each group occurred.

RESULTS

Species–area relationships

The six data sets combined held records of 23 540 carabid beetles belonging to 141 species. Of these, 2983 individuals (13%) and 48 species (34%) were classified as dry-grassland specialists. Preliminary analyses showed that both trophic rank and flight ability, but not body size, significantly altered the SAR of dry-grassland specialists (Appendix C). Because trophic rank had the most significant effect on SAR, further analyses focused primarily on this trait (but see *Discussion*). A full analysis of all three habitat affinity groups revealed that both species richness and activity density were best explained by models including calcareous grassland size, trophic rank, and a measure of additional calcareous grassland in the landscape (Table 2; Appendix D). Additional calcareous grass-

TABLE 3. Model averages for the fixed-effects parameters in the best three generalized linear mixed models for species richness of carabid beetles; the estimate is the effect size on a natural log scale.

Fixed-effect parameter, by habitat preference	Estimate	SE	<i>z</i>	<i>P</i>
Dry-grassland specialists				
(Intercept)	−4.47185	1.27327	−3.510	0.001
Area	0.48402	0.11654	4.153	<0.001
Trophic rank shift	−0.47318	3.38273	−0.140	0.889
Phytophagous species	4.46496	1.40646	3.174	0.002
Area × Trophic rank shift	−0.16320	0.31918	−0.512	0.608
Area × Phytophagous species	−0.39842	0.13283	−2.999	0.003
Additional calc. grassland, 500 m	0.04914	0.01597	3.076	0.002
Additional calc. grassland, 1000 m	0.03574	0.01578	2.265	0.023
Open-habitat generalists				
(Intercept)	0.75861	0.437154	1.747	0.120
Area	0.07929	0.038182	2.075	0.046
Trophic rank shift	−1.41957	1.068687	−1.328	0.184
Phytophagous species	0.26232	0.64351	0.4073	0.684
Area × Trophic rank shift	−0.06933	0.100987	−0.686	0.492
Area × Phytophagous species	−0.11146	0.061102	−1.824	0.068
Additional calc. grassland, 500 m	0.03654	0.009807	3.726	<0.001
Additional calc. grassland, 1000 m	0.02017	0.009572	2.107	0.035
Forest and wet-grassland specialists				
(Intercept)	1.43105	0.403642	3.555	0.001
Area	0.04255	0.03525	1.206	0.235
Trophic rank shift	−2.87945	1.467678	−1.962	0.050
Phytophagous species	−0.63522	0.837104	−0.759	0.448
Area × Trophic rank shift	−0.01780	0.137981	−0.129	0.897
Area × Phytophagous species	−0.11725	0.080532	−1.456	0.145
Additional calc. grassland, 500 m	0.01727	0.009739	1.774	0.076
Additional calc. grassland, 1000 m	0.01738	0.009585	1.813	0.070

Notes: The base model represents zoophagous carabid beetles. Trophic rank shift refers to species with zoophagous larvae and phytophagous adults. Phytophagous refers to species that are phytophagous throughout their life cycle. Addition of calcareous (calc.) grassland was made at two scales: a radius of 500 m or 1000 m. Boldface highlights *P* values < 0.05.

land in the landscape significantly increased the local species richness for both dry-grassland specialists and open-habitat generalists, but not for forest and wet-grassland specialists (Table 3). This effect was most pronounced when only including additional calcareous grassland within a 500 m radius, and was only marginally significant when including all additional calcareous grassland within a 1000 m radius. Activity density of dry-grassland specialists was not affected by additional calcareous grassland nearby (Table 4). However, activity density of open-habitat generalists increased with additional calcareous grassland especially at the 500-m scale.

Trophic rank

Trophic rank significantly affected species–area relationships, but only for dry-grassland specialists (almost so for generalist species) (Fig. 1, Table 3). Within the dry-grassland specialists, phytophagous species were less affected by calcareous grassland size than were zoophagous species (significant interaction: area × phytophagous). The SAR for species that shift in trophic rank during their life cycle did not differ from that for zoophagous species (Fig. 1, Table 3). It should be noted, however, that the number of species shifting in trophic rank was limited (six species in total). Activity density was affected by trophic rank in

much the same way as species richness (Fig. 2, Table 4). An additional GLMM revealed that there was also a significant effect of trophic rank on SAR within dry-grassland specialists with medium and good dispersal ability (Appendix E). This demonstrates that the effect of trophic rank on SAR is not purely a reflection of the greater number of flightless species among zoophagous carabid beetles. Based on our model parameter estimates, we calculated predicted total activity density of zoophagous and phytophagous carabid beetles in small, medium, and large calcareous grasslands. This revealed that total activity density of zoophagous species increases sharply with calcareous grassland area, whereas the activity density of phytophagous species shows a slight decline (Table 5).

Dispersal ability

The range of occupied grassland sizes differed significantly between dispersal groups for zoophagous dry-grassland specialists (Levene's test; $F_{2,54} = 4.53$, $P = 0.015$), but not for other trophic groups or for habitat generalists (Levene's test; $F < 0.50$, $P > 0.50$). Dry-grassland specialists with poor dispersal ability were only found in the largest sites, whereas dry-grassland specialists with good dispersal ability were found in the widest range of sites (Fig. 3).

TABLE 4. Model averages for the fixed-effects parameters in the best three generalized linear mixed models for activity density (natural log scale) of carabid beetles; the estimate is the effect size on a natural log scale.

Fixed-effect parameter, by habitat preference	Estimate	SE	<i>z</i>	<i>P</i>
Dry-grassland specialists				
(Intercept)	-4.17339	1.30855	-3.188	0.002
Area	0.45206	0.12044	3.753	<0.001
Trophic rank shift	-0.34450	2.84219	-0.121	0.904
Phytophagous species	5.65831	1.41822	3.989	<0.001
Area × Trophic rank shift	-0.12237	0.26767	-0.457	0.648
Area × Phytophagous species	-0.49899	0.13455	-3.708	<0.001
Additional calc. grassland, 500 m	0.02512	0.01551	1.620	0.105
Additional calc. grassland, 1000 m	0.02090	0.01543	1.354	0.176
Open-habitat generalists				
(Intercept)	0.57947	0.47250	1.235	0.260
Area	0.07121	0.04156	1.712	0.096
Trophic rank shift	-0.48149	0.82524	-0.584	0.560
Phytophagous species	0.47163	0.68359	0.690	0.490
Area × Trophic rank shift	-0.06701	0.07679	-0.873	0.383
Area × Phytophagous species	-0.10815	0.06397	-1.690	0.091
Additional calc. grassland, 500 m	0.03359	0.01047	3.209	0.001
Additional calc. grassland, 1000 m	0.02625	0.01027	2.557	0.011
Forest and wet-grassland specialists				
(Intercept)	0.61987	0.49592	1.258	0.234
Area	0.07720	0.04367	1.767	0.082
Trophic rank shift	-1.10087	1.19834	-0.919	0.358
Phytophagous species	0.20281	0.81556	0.249	0.804
Area × Trophic rank shift	-0.09551	0.11373	-0.840	0.401
Area × Phytophagous species	-0.13254	0.07773	-1.705	0.088
Additional calc. grassland, 500 m	0.02071	0.01126	1.839	0.066
Additional calc. grassland, 1000 m	0.02402	0.01114	2.156	0.031

Notes: See Table 3 for definitions of model terms. Activity density (counts of individuals, which are affected by both a species' density and its activity pattern) is not a measure of absolute density, but reflects the impact of a species group because it represents the encounter rate or "effective" abundance (Den Boer 1977). Boldface highlights *P* values < 0.05.

DISCUSSION

Our meta-analysis demonstrates that the increase in carabid beetle species richness and activity density with increasing area depends on both habitat affinity and trophic rank of the species. This is the first time that the effect of trophic rank on SARs has been studied within a single monophyletic group. Previous studies have all used phylogenetically highly divergent taxa such as plant–herbivore or host–parasite systems (Tscharnkte et al. 2002b, Van Nouhuys 2005). Our study thus demonstrates that the effect of trophic rank on SARs extends beyond herbivores and parasites and is not confounded by other factors specific for host–parasite and plant–herbivore systems. We also demonstrate that the dependence of species on large, single sites increases with decreasing dispersal ability. Moreover, additional habitat in the surrounding landscape has a positive effect on local species richness, but not on activity density.

Habitat affinity

It has repeatedly been shown that SAR theory, which was initially developed for real islands, also applies to "islands" of a specific biotope (e.g., calcareous grassland) surrounded by other land use types (Davies et al. 2000, Steffan-Dewenter and Tscharnkte 2000, Hanski et

al. 2013). However, in contrast to real islands, the matrix surrounding biotope "islands" may be suitable habitat for generalist species, making SARs less applicable (Davies et al. 2000, Shepherd and Brantley 2005, Driscoll et al. 2013). In line with this, we showed that carabid species richness only strongly increased with calcareous grassland size for dry-grassland specialists. This demonstrates the importance of adopting an organism-centered understanding of landscapes and habitat patches (Shepherd and Brantley 2005), for example by incorporating species' habitat affinity (see also De Vries et al. 1996). However, one difficulty with using habitat affinity classes is that habitat affinity cannot be measured independent of a species' environment (see Violle et al. 2007). Habitat affinity scores are generally derived from distribution records and therefore depend on the availability of records and on the structure of the landscape in which they are recorded. Species may therefore seem to have a wider tolerance of habitat conditions than they actually have, because they can occur both in seminatural grassland and on arable land, but only under specific circumstances. This seems to be the case for at least some of the generalist species in our study, because generalist zoophagous carabid beetle richness increased with calcareous grassland area. Apparently some of the species classified as generalists,

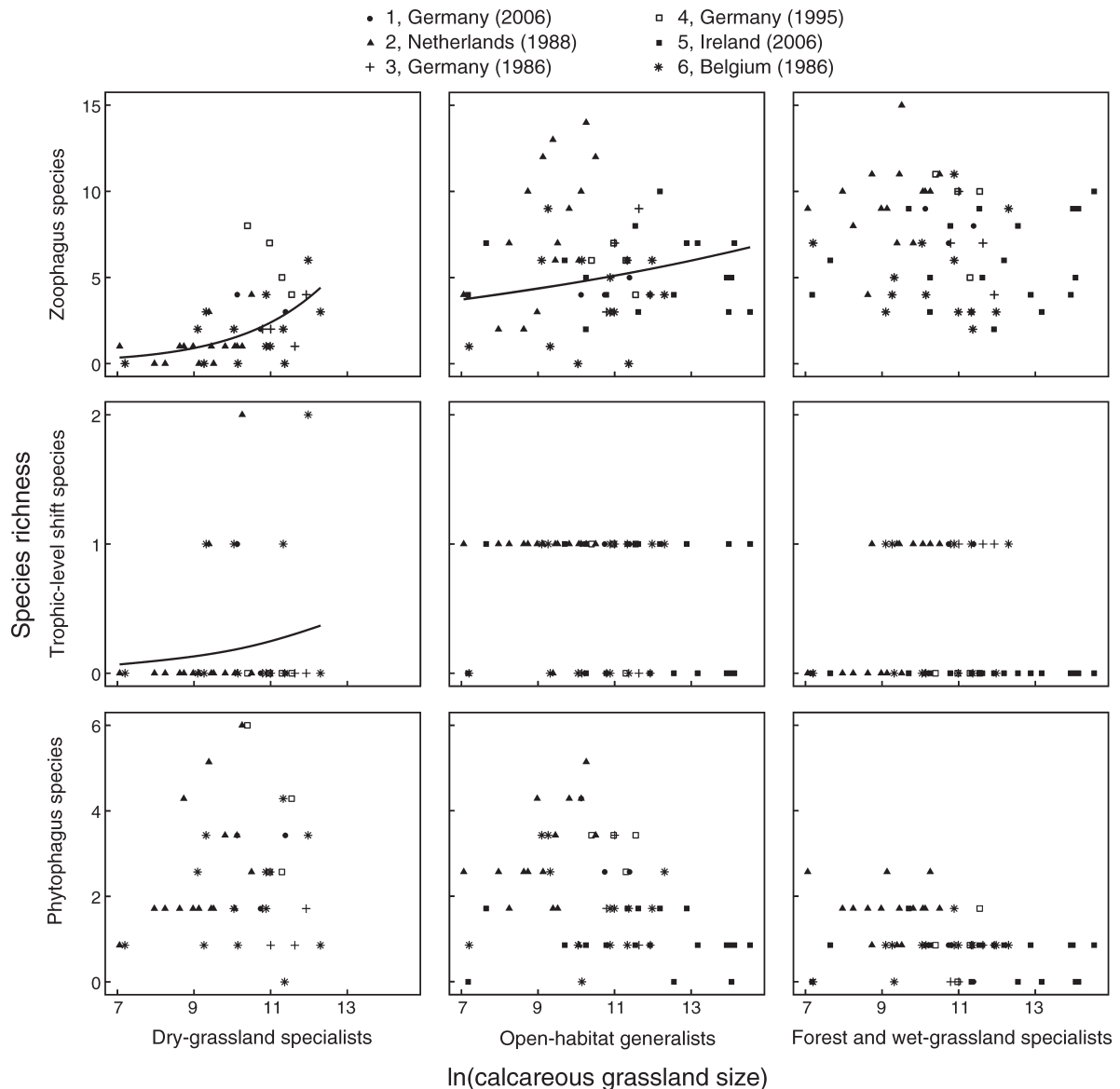


FIG. 1. Species richness of zoophagous species (upper panels), phytophagous species with zoophagous larvae (middle panels), and phytophagous species (lower panels) as a function of calcareous grassland size (natural log scale, originally measured in m^2). Species are grouped by habitat affinity: typical dry-grassland species, generalist open-habitat species, and wet-grassland and forest species. Fitted lines (Poisson GLMM, generalized linear mixed models) are plotted where significant ($P < 0.05$) effects of calcareous grassland size on species richness were found (see Table 2).

and assumed to be capable of surviving in the mainly arable matrix, were still more or less restricted to calcareous grassland. As long as the causal mechanism underpinning a species' habitat affinity remains unknown, it will remain difficult to make accurate predictions.

Landscape context

Additional calcareous grassland in the vicinity had a positive effect on species richness for dry-grassland specialists in our study, as would be expected from island biogeography theory (MacArthur and Wilson

1967). Surprisingly, this effect was also found for habitat generalists, indicating again that the surrounding landscape matrix does not form suitable habitat for all generalists. The spatial extent of the effect of additional calcareous grassland was limited to a few hundred meters, demonstrated by the stronger effect of additional calcareous grassland at the 500-m compared to the 1000-m scale. In addition, the positive effect of additional calcareous grassland in the landscape proved to be much weaker than the effect of increased area. Additional calcareous grassland in the landscape only affected species richness, not activity density, of dry-

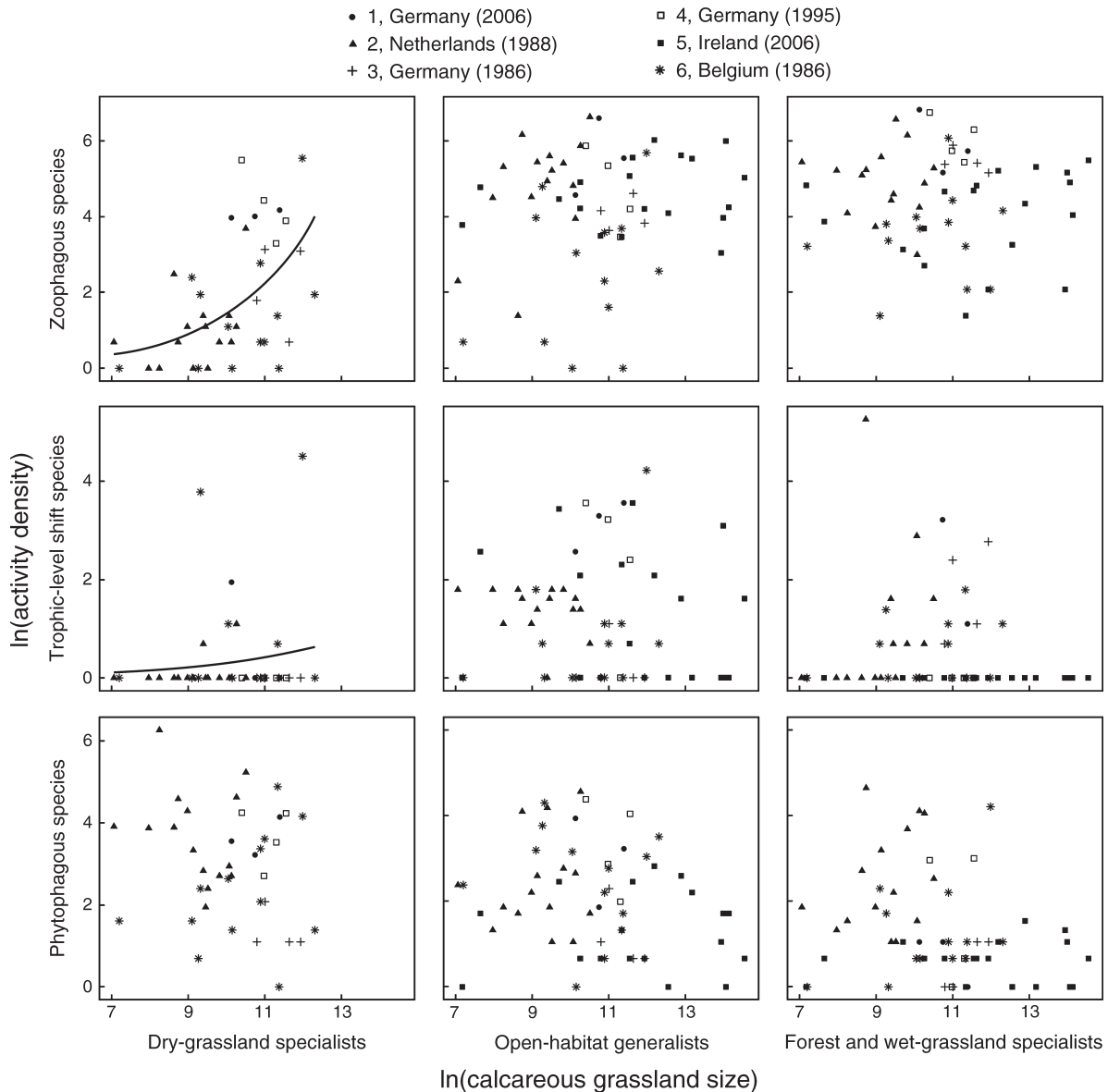


FIG. 2. Activity density (natural log scale) of zoophagous species (upper panels), phytophagous species with zoophagous larvae (middle panels), and phytophagous species (lower panels) as a function of calcareous grassland size (natural log scale, originally measured in m^2). Activity density (counts of individuals, which are affected by both a species' density and its activity pattern) is not a measure of absolute density, but reflects the impact of a species group because it represents the encounter rate or "effective" abundance (Den Boer 1977). Species are grouped by habitat affinity: typical dry-grassland species, generalist open-habitat species, and forest and wet-grassland species. Fitted lines (Poisson GLMM) are plotted where significant ($P < 0.05$) effects of calcareous grassland size on activity density (natural log scale) were found (Appendix D: Table D1).

grassland specialists. This indicates that the influx of individuals from these additional areas is too small to affect local population densities, but high enough to offer increased recolonization chances after local extinction, contributing to community resilience.

Significance of species–area relationships

The slope of SARs may vary with sampling intensity (Hill et al. 1994, Cam et al. 2002). More intensive sampling gives a better estimate of the true species

richness, especially in species-rich sites, giving rise to steeper SARs. Therefore, the differences in sampling duration (between 55 and 730 days) and in the number of traps per site (between 10 and 20) between our data sets may have affected the SAR slopes that we found (sampling intensity was identical across sites within data sets). In our models, we accounted for any differences between data sets by including data set as a random variable. However, not all variance attributed to data set was caused by sampling intensity, because our data sets

also differed in other respects (e.g., geographic region, landscape context, regional species pool, climate, and sampling year). Because of this, it is difficult to estimate the exact effect of sampling intensity on the differences in SAR slopes between data sets in our study. An effect of sampling intensity is most likely in the Irish data set, which had the lowest sampling duration (55 days, compared to 185 or more days for each of the other data sets). However, the Irish data set also deviates most from the other data sets with respect to landscape and climate and has the most restricted regional species pool, making it impossible to attribute differences in SAR to any of these factors in particular. Overall, sites included in our study were sampled relatively intensively, considering that many studies use sampling periods of ~28 days (see, for example, Mayr et al. 2007, Wamser et al. 2012). Therefore, we expect that effects of sampling intensity on our overall results are limited. This is corroborated by the fact that the SARs found in our study are very similar in slope to those previously reported for other arthropods. The z value (slope of the SAR) we found for zoophagous dry grassland specialists (0.48) is identical to the z value reported by Tscharnke et al. (2002b) for monophagous butterflies in a similar arable land–calcareous grassland landscape. A study conducted on real islands reported a z value of 0.36 for total carabid beetle richness (Nilsson et al. 1988). These slopes are ~10 times higher than those reported for birds, mammals, and amphibians in a global study by Storch et al. (2012). This most likely reflects the smaller spatial scale at which arthropods operate compared to vertebrate taxa. Importantly, the high z values for arthropods imply that even small decreases in habitat size can have a significant ecological impact, especially if groups of species are differentially affected. Our analysis demonstrated such variable responses for species differing in trophic rank and dispersal ability. We were able to demonstrate that both characteristics had an independent effect, i.e., effects were not solely caused by collinearity between dispersal ability and trophic rank. Poor and good dispersers occurred in many different genera, making it unlikely that observed patterns were solely due to phylogeny rather than dispersal ability. Similarly, habitat affinity classes were generally unrelated to phylogeny, with dry-grassland specialists and habitat generalists found in most genera. Trophic rank was more strongly related to phylogeny, with only *Amara* (Pterostichinae), *Harpalus*, and *Ophonus* species (Harpalinae) being phytophagous, although other genera within those subfamilies belong to different trophic ranks. The species classified as zoophagous are of very diverse phylogenetic origin. Species with an ontogenetic shift in trophic rank, which are phylogenetically closely related to fully phytophagous species, responded in the same way as zoophagous species. These are strong indicators that the observed responses are causally related to trophic rank, rather than to underlying

TABLE 5. Calculations of total activity density of carabid beetles of different trophic ranks in small (1-ha), medium (10-ha), and large (100-ha) chalk grasslands, based on parameter estimates derived from GLMM analysis (see Table 3).

Trophic rank and habitat affinity	Site area		
	1 ha	10 ha	100 ha
Zoophagous beetles			
Dry grassland	3	16	2309
Generalist	30	55	110
Forest and wet grassland	49	107	274
Total	81	177	2693
Phytophagous beetles			
Dry grassland	16	12	9
Generalist	7	6	5
Forest and wet grassland	4	4	3
Total	28	22	18

phylogenetic constraints or other traits associated with phylogeny.

Trophic rank modulates SAR

Our results clearly demonstrate that zoophagous carabid beetles respond more strongly to calcareous grassland area than do phytophagous species. Our results also indicate that phytophagous species with zoophagous larvae respond in a way similar to zoophagous species, rather than phytophagous species, to which latter group they are usually assigned (e.g., Ribera et al. 1999, Vanbergen et al. 2010). However, the number of species shifting in trophic rank during their life cycle is limited (six species in our data set), so these results should be interpreted with caution.

An effect of trophic rank on SAR was previously predicted (Holt et al. 1999) and empirically demonstrated (Steffan-Dewenter and Tscharnke 2000, Van Nouhuys 2005). However, these studies argued that the slope of SARs should only increase with trophic rank for food specialists (e.g., specialist parasitoids or monophagous consumers) because generalists can compensate for low availability of one food source by utilizing alternative sources, hence showing less population fluctuation. Additionally, food generalists, being able to utilize multiple food sources, are predicted to have higher population densities (Brown 1984). In contrast, our results suggest that trophic rank per se, i.e., irrespective of food specialization, affects the slope of SARs. The zoophagous carabid beetles, for which we have found an increased dependence on calcareous grassland area, generally feed on a wide array of prey species (Thiele 1977, Turin 2000) and are thus food generalists. A wide range of food sources may be insufficient to buffer against adverse conditions when all food sources fluctuate in a synchronized manner, e.g., as a response to drought or other adverse weather conditions. Moreover, population densities, which affect extinction rates, were previously found to be lower for zoophagous

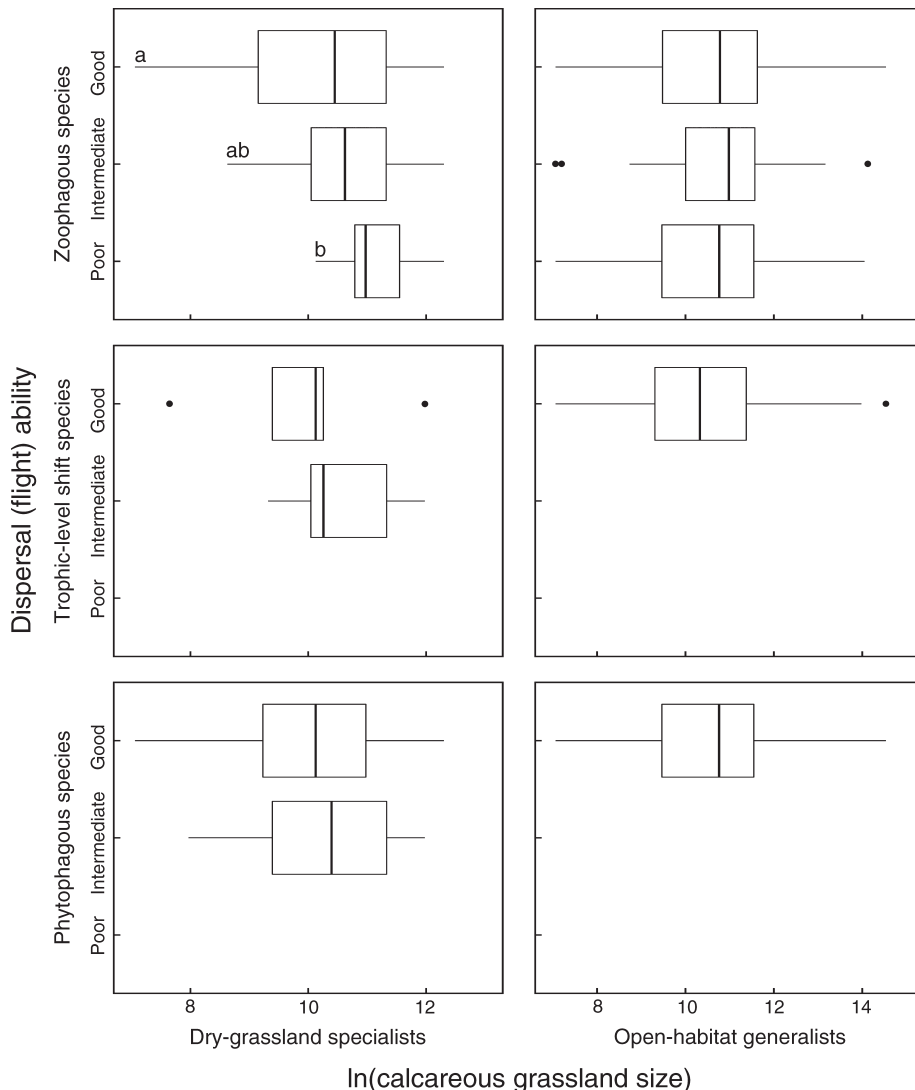


FIG. 3. Boxplots of occurrences of typical dry-grassland and generalist open-habitat carabid beetles in calcareous grasslands of varying sizes (natural log scale, originally measured in m^2), by flight ability. Different lowercase letters indicate significantly different variances of calcareous grassland size between flight ability groups. Boxplot components: line in the box, median; box endpoints, first and third quartiles (the 25th and 75th percentiles); whiskers extend from the box to the highest and lowest value that is within $1.5 \times IQR$ (interquartile range) of the box; points beyond the end of the whiskers are outliers (as specified by Tukey).

species than for phytophagous species across a wide array of species with differing food specialization (Verberk et al. 2010). Several previous studies (Holt et al. 1999, Steffan-Dewenter and Tscharntke 2000, 2002, Van Nouhuys 2005) did not find strong SARs for higher trophic rank generalists, in contrast to our results. In both parasitoids and butterflies, the two main groups previously used to study effects of trophic rank on SAR, food specialization, however, is strongly correlated with habitat specialization and often also with dispersal power (Bink 1992, Van Nouhuys 2005). Thus, the differences found between food generalists and specialists may represent a different perception of the landscape (more continuous vs. highly fragmented), rather than a different area dependence arising from

food specialization. If trophic rank per se, rather than food specialization, affects SARs, the impact of habitat size on trophic interactions may be larger than previously anticipated. This conclusion resonates well with studies on the effects of forest fragmentation, which have demonstrated that carnivores respond more strongly to forest fragmentation than do lower trophic ranks, independent of food specialization (Didham et al. 1998, Davies et al. 2000). The distinction between food specialization and habitat specialization may seem trivial, especially because they are frequently interrelated. However, several authors have previously argued that keeping them separate is important to better understand large-scale patterns (Gaston et al. 1997, Verberk et al. 2010). Our results also suggest vital

repercussions for the importance of the landscape context. If only food specialists depend on larger sites, the number of generalist predators in a small site would be independent of the surrounding landscape. However, if the area dependence of species is governed by habitat affinity, species richness and density of predators in small sites would decline sharply with decreasing suitability of the surrounding landscape. This would create potential for strongly disrupted food chains in isolated habitat fragments surrounded by a hostile matrix. This could, for example, lead to spillover effects of phytophagous pest species into agricultural land (Kruess and Tscharntke 1994, Tscharntke et al. 2005). This potential is also illustrated by our calculation of the predicted total activity density of zoophagous and phytophagous carabid beetles in calcareous grasslands of different sizes. Although activity density is not a measure of absolute density (Thiele 1977), it does reflect the impact of a species group because it represents the encounter rate or “effective” abundance (Den Boer 1977). Our calculation thus demonstrates that predation pressure in small sites can be greatly reduced, whereas no such reduction was found for phytophagous species. This adds to recent concerns that habitat loss may lead to serious community instability and potentially threatens ecosystem service provision (Spiesman and Inouye 2013).

Dispersal ability

Dispersal ability affects species’ vulnerability to habitat isolation (Den Boer 1990a, Wamser et al. 2012). We demonstrated that this also leads to a restriction of poor dispersers to larger sites, at least for zoophagous, dry-grassland species. This is in line with previous studies by De Vries et al. (1996). Although dispersal ability is partly correlated with body size in carabid beetles (all large species are flightless), we were able to demonstrate that the effect found here is caused by flight ability itself, because we found no significant effect of body size on SAR.

Implications

Our results demonstrate that the effect of calcareous grassland area on species richness of carabid beetles is affected by trophic rank and habitat affinity (affecting local extinction chances) in combination with dispersal ability (affecting recolonization rates). Interestingly, recent reviews found insufficient or inconsistent proof for the importance of all three of these species’ characteristics for SAR (Henle et al. 2004, Van Nouhuys 2005). This apparent discrepancy is caused by the fact that species’ characteristics do not operate independently (Davies et al. 2004, Van Kleef et al. 2006, Verberk et al. 2013). For example, traits related to recolonization rates (dispersal ability) only become important for species exhibiting characteristics that increase their local extinction chances (combination of zoophagous and habitat specialist traits). In addition,

we found that the landscape context modulates the effect of specific species’ characteristics. Additional patches of calcareous grassland in the surrounding landscape can supplement the biodiversity of a particular location, but only with species with good dispersal ability and only over short distances. The quality of the surrounding landscape will affect the extent to which habitat generalists can inhabit the matrix and, hence, the extent to which they are limited by the area of one biotope type. In a hostile landscape, habitat generalists would be expected to encounter similar restrictions as habitat specialists, causing them to respond in a similar way to site size.

Our results indicate that of all dry-grassland specialists, zoophagous species are disproportionately affected by habitat fragmentation. In the six data sets, spanning four northwestern European countries, zoophagous dry-grassland specialists with poor dispersal ability were virtually absent from calcareous grasslands smaller than 5 ha. Trophic interactions thus may be seriously disrupted in smaller sites, especially if they are surrounded by a hostile matrix. This highlights the need to conserve calcareous grassland patches of at least several hectares in size.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-0082.1.sm>